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AN EARLY PAPER ON MAIZE CROSSES

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IN the writer's opinion the paper of McCluer, entitled "Corn Crossing,"[1] has lacked adequate appreciation by later investigators. This paper is referred to by East (3), Shull (7) and Collins (1) in various articles, but only with reference to McCluer's observations on the superiority of F_1 hybrids in point of yield, as compared with their parents. The other matter of genetic interest in the paper seems to have attracted little attention, perhaps because of the more extensive earlier experiments ('89–91) of Kellerman and Swingle (4), and the more important later ones of Correns (2).

However, with respect to the superior yield of F_1 hybrids, McCluer's paper exceeds in interest the more frequently quoted ones of Morrow and Gardner[2] in respect to the wider variety of types selected for crossing, and especially in the fact of the progeny of the F_1 plants having been followed out in the yields of the F_2 generation, which, in all but a very few cases, were found to be distinctly less than the yields of the F_1 plants. This seems to have been, historically speaking, the first demonstration of the inferiority in yield of F_2 segregates, as compared with first generation hybrids. McCluer's experiments involved a wider range of types of maize than did those of Morrow and Gardner, and comprised dent, sweet,

[1] Ill. Ex. Sta. Bull. 21, May, 1892.

[2] Ill. Ex. Sta. Bull. 25, 179–80, and 31, 359–60.

pop and soft corn varieties in eighteen different crosses. He was thus enabled to make observations on the inheritance of characters other than those resulting in yield.

In 1889 McCluer began his hybridization work with corn, crossing a number of strains of dent maize, without at first, however, making crosses between varieties of different colors. In addition he utilized the following characters in thirteen crosses made in 1889, and in five crosses made in 1890 obtained in the former year 36 and in the latter year 158 ears.

Sugary endosperm	×	starchy endosperm.
White endosperm	×	yellow endosperm and the reciprocal.
Starchy endosperm	×	corneous endosperm and the reciprocal.
Corneous endosperm	×	sugary endosperm.
Non-colored aleurone	×	purple aleurone.

Expressing these crosses in the following notation, according to presence and absence, for convenience, without regard to the actual gametic composition of the parents, which of course can only be inferred, we have:

A. Yellow endosperm.
a. White endosperm.
B. Starchy endosperm.
b. Sugary endosperm.
C. Colored aleurone.
c. Non-colored aleurone.
C. Corneous endosperm.

McCluer's crosses then classify according to the formulas on the following page.

Leaving it understood that this is simply a classification in shorthand formulas, of the visible characters, without predicating their gametic composition, which was unknown to McCluer, since he far antedated the days of pure lines, Mendelism and factorial analyses, we are struck by the number of factors with which he experimented, and with his clean observations on the results. Being a horticulturist, he was led to be interested in these various types of maize, to which Morrow and Gardner, as agronomists, gave no attention.

Cross	Phenotype Characters	Variety		Phenotype Characters	Variety
1	abc	Mammoth	×	ABc	Leaming
2	abc	Triumph	×	ABc	"
3	abc	8-rowed	×	ABc	"
4	abc	Mammoth	×	Abc	Golden Coin (Sweet)
5	abc	Triumph	×	Abc	" " "
6	abc	8-rowed	×	Abc	" " "
7	abc	Mammoth	×	Abc	Stowell's Evergreen
8	abc	Triumph	×	Abc	" "
9	abc	8-rowed	×	Abc	" "
10	abc	White Dent (unnamed)	×	ADc	Queen's Golden Pop
11	ADc	Queen's Golden Pop	×	ABc	White Dent (unnamed)
12	ADc	" " "	×	abC	Black Mexican
13	ABc	White Dent (unnamed)	×	abC	" "
14	ABc	Brazilian Flour	×	Abc	Gold Coin (Sweet)
15	ADc	Pearl (pop)	×	ADc	Queen's Golden (Pop)
16	aBc	Burr's White Dent	×	aBc	Brazilian Flour
17	aBc	Yellow Dent variety	×	aBc	White Dent variety
18	aBc	White Dent variety	×	aBc	Yellow Dent variety

McCluer found no xenia effect to be produced, where, as he says, ears "of the same color" but of different types are crossed.

The typical ear of Stowell's Evergreen differs very decidedly from typical ears of either 8-rowed, Triumph or Mammoth, but the ears produced by pollen of Stowell's on either of the others, did not differ from the female type in any way, more than did many ears left to be fertilized naturally.

In other words, he observed that the "maternal" tissues beyond the endosperm were not affected by the crossing.

McCluer found that in F_1 ears, of crosses between yellow and non-yellow endosperm, the dominant yellow of the F_1 kernels was never as dark as in the yellow parent, whether the latter were the pollen or the seed parent. This fact was observed in crosses 1, 2, 3, 10, 11, 13, 17 and 18. Since McCluer remarks that the effect was not uniform in yellow dent × white dent crosses and their reciprocals, he may in these cases have unconsciously run across the phenomenon of two yellows, as reported in 1911 by East and Hays (3), pp. 46–56. It is probable, however, that most of the instances were cases of the heterozygous yellows, being lighter than the homozygous

yellows, as reported by East and Hayes, *loc. cit.*, pp. 55–6. In McCluer's crosses, 14, 17 and 18 at least, he was evidently working with endosperm color factors, the behavior of which was identical with those reported by East and Hayes in their crosses as given in the citation above.

McCluer made a considerable number of observations on xenia, but remarks (italics mine), "*The results obtained from planting crossed seed have been of more importance than the immediate effect of crossing,* not so much in themselves perhaps as in the conclusions which may be drawn from them." Such a point of view could only have been arrived at by one with something of an instinct for genetic studies.

McCluer remarks upon the great uniformity of what we should call F_1 hybrids. He says:

> Of 142 plots planted with sweet corn, pop-corn and their crosses, it is safe to say, there was as much uniformity in any one of the crossed plots, as in any, and very much more than was found in most of the plots planted with pure varieties.

Some interesting notes were made as to the characteristics of some of the F_1 plots. For example, it seems that the plots in which Leaming was used as the pollen parent decidedly resembled that parent; that in crosses between Queen's Golden × White Dent, the F_1 plants resembled the pollen parent, whereas in the reciprocal cross, the plants were intermediate between the two parents. An interesting result came from the cross between Queen's Golden and Pearl pop-corn. The stalks were intermediate between the parents, but larger than the average of the two parents. This characteristic extended to the growth of the cob, so that the F_1 ears were distinctly larger than the average of the ears of either of the parents—a fact very well illustrated in Plate 2 of the bulletin. Plots of F_1, hybrids between White Dent × Black Mexican, decidedly resembled the white dent. An extraordinary result seems to have been obtained in this cross. The F_1 seeds—*i. e.*, the seeds of the white dent ear pollinated with Black Mexican pollen, show the usual

dominance of purple aleurone in the F_1 kernels. But the starchy character, ordinarily completely dominant in F_1 seeds of starchy × sugary endosperm crosses, is not dominant in all the kernels. So far as the F_1 ear illustrated on Plate 1 indicates, on which there are four tolerably complete rows in sight, there is a ratio of wrinkled to smooth kernels of 73:50, or approximately 1:1, which would go to indicate that the seed parent was probably heterozygous as to starchy endosperm. The wrinkled seeds from this ear produced ears, to judge again from the plate, for there is no detailed description, that were pure wrinkled in their kernels, whereas the smooth kernels from the F_1 ear produced ears on which both smooth and wrinkled F_2 kernels were borne. Three such ears are illustrated. On each of these ears three complete rows of kernels are visible in the illustration. Counts of these kernels, as nearly as they can be made from the illustrations, show: In ear No. 3 (*i. e.*, the ear showing the immediate effects of the cross and bearing the F_1 kernels) the ratio of smooth seeds to wrinkled seeds is as 73:50.

It was eight years later that the papers of Mendel were rediscovered, and at this time no scientific knowledge of the genetic behavior of corn existed at all. McCluer obtained, however, very definite evidence that the ears "borne by hybrid corn plants grown the first year from the cross," as he puts it, or as we should say to-day, plants of the F_1 generation, were larger on the average than the average ear borne by the parents, and that the yield was greater. Taking McCluer's tabulations of his results on p. 97 of Bull. 21, and revising its notation to correspond with present usage, we have the data given on page 102.

From this early experiment the result of crossing, so far as the yield of the F_1 generation is concerned, is fairly well indicated, since in fourteen cases out of eighteen the F_1 hybrids yield more than the average of the two parents, although in only seven cases did the yield of the F_1 hybrid exceed that of both the parents. McCluer also emphasizes the inferior condition of the self-fertilized plots.

Cross	Wt. (Oz.) of 10 Ears of the Male Parent	Wt. (Oz.) of 10 Ears of the Female Parent	Av. Wt. (Oz.) 10 Ears of the Two Parents	Wt. (Oz.) of 10 Ears Borne by the F_1 Generation (F_2) Seed
Queen's Golden (1) × White Dent ...	34.50	81.00	57.75	76.00
White Dent × Queen's Golden.......	81.00	34.50	57.75	64.00
Queen's Golden × Black Mexican (2).	34.50	36.00	35.25	47.50
Common Pearl (1) × Queen's Golden.	27.50	34.50	31.00	42.00
Mammoth (2) × Leaming (3)........	61.50	87.50	74.50	91.00
Mammoth × Leaming	61.50	87.50	74.50	82.00
Mammoth × Leaming	61.50	87.50	74.50	80.50
Triumph × Leaming	46.50	87.50	67.00	83.00
Eight-rowed (2) × Leaming	41.00	87.50	64.25	72.00
Brazilian Flour Corn × Gold Coin (2).	39.00	63.00	57.00	78.00
White Dent × Black Mexican.......	81.00	36.00	58.50	51.00
Eight-rowed × Stowell's Evergreen (2)	41.00	57.50	49.25	47.00
Triumph (2) × Stowell's Evergreen...	46.50	57.50	52.00	52.50
Mammoth × Stowell's Evergreen	61.50	57.50	59.50	61.00
Gold Coin × Stowell's Evergreen.....	62.50	57.50	60 00	62.50
Triumph × Gold Coin	46.50	62.50	54.50	58.50
Eight-rowed × Gold Coin	41.00	62.50	51.75	56.00
Eight-rowed × Gold Coin	41.00	62.50	51.75	58.00
Average..........................	50.50	63.30	57.20	64.50

(1) Pop corn, (2) sweet corn, (3) dent corn.

Plots grown from self-fertilized seed, were in most cases notably inferior in size and vigor to the plots grown from crossed seed, or from seed simply selected. The table does not give so convincing an illustration of the bad effects of self-fertilization, as the plots themselves did when growing, or as the corn did when husked and thrown into piles. One plot from self-fertilized seed had nearly half the stalks deformed in such manner that instead of standing up straight, they turned off nearly at a right angle, at or near the joint where the ear was produced, thus throwing the tassel on a level with or below the ear. Many of the tassels were very deficient in pollen. In another plot from self-fertilized seed, nearly all the tassels were abortive. All the plots from self-fertilized seed produced a greater proportion of barren stalks, and of poorly filled ears, than the plots of the same varieties, either from crossed seed or from seed naturally fertilized. The table giving the weight of ten selected ears of corn from self-fertilized seed, and of ten ears from crossed or selected seed, does not give a correct idea of the inferiority of the corn from the self-fertilized seed, because it does not take into account, either the greater proportion of barren stalks, or of small poorly filled ears (pp. 96 and 98).

The results of this experiment at the time simply led to the conclusion that continued selection of corn, leading to a certain amount of inbreeding, was likely, like close

fertilization consciously practised, to lead to "deterioration," and that cross fertilization, as it occurs ordinarily in corn, is desirable for the best results. No suggestion is offered by McCluer as to utilizing this fact in a practical way. It remained for Messrs. Morrow and Gardner, also of the Illinois Station, to derive this conclusion from their experiments. In Bulletin 25 of the Illinois Station, pp. 179–180, results are given of crosses made between dent corn varieties exclusively, which, while less extensive and varied than McCluer's, are confirmatory of his experiments. The following table, adapted from Bull. 25, p. 180 (1893), presents these results:

Variety	Bu. Air-dry Corn per Acre	
Burr's White	64.2	
Cranberry	61.6	
Average	62.9	
Cross		64.1
Burr's White	64.2	
Helm's Improved	79.2	
Average	71.7	
Cross		73.1
Leaming	73.6	
Golden Beauty	65.1	
Average	69.3	
Cross		86.2
Champion White Pearl	60.6	
Leaming	73.6	
Average	67.1	
Cross		76.2
Burr's White	64.2	
Edmunds	58.4	
Average	61.3	
Cross		78.5

In each of the above cases the yield from the cross exceeded the average yield of the two parents, although not in all cases exceeding that of each parent.

In Bulletin 31, pp. 359–60 (1894), the result of Morrow and Gardner's second experiment in crossing corn is given.

Champion White Pearl	37.3	
Burr's White	38.6	
Average	38.0	
Cross		28.4
Leaming	34.6	
Burr's White	38.6	
Average	36.6	
Cross		41.7
Edmund's	28.3	
Murdock	35.7	
Average	32.0	
Cross		41.4
Edmund's	28.3	
Burr's White	38.6	
Average	33.5	
Cross		37.8

In three out of the four cases above the cross out-yielded the average yield of the two parents.

Some observations were made by McCluer, (p. 86), as to effect of crossing on the number of rows of kernels, the results being an approximately intermediate condition in the F_1 hybrids with respect to this character.

Parents	No. of Rows
Leaming	18–24
Mammoth Sweet	12–16
F_1 hybrids	14–18
Leaming	18–24
Eight-rowed Sweet	8
F_1 hybrids	10–14
Leaming	18–24
Triumph	8
F_1 hybrids	10–16

McCluer remarks upon the difference in reciprocal pop-corn—dent-corn crosses, to the effect that when the pop corn was used as a pollen parent, the F_1 kernels were more flinty than when the dent corn was used as the pollen parent.

So far as the writer knows, McCluer is the first person known to have made a cross between two different types of corn, who paid close enough attention to the results of such a cross to lead him to illustrate the parent ears, the

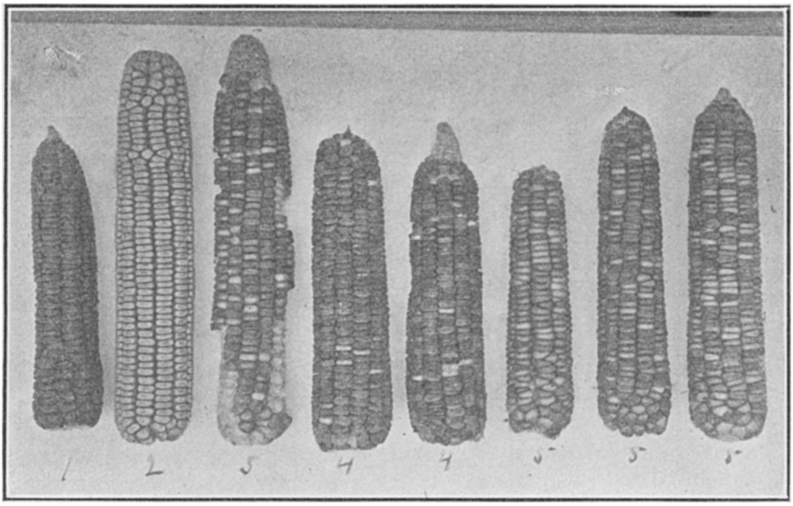

FIG. 1.

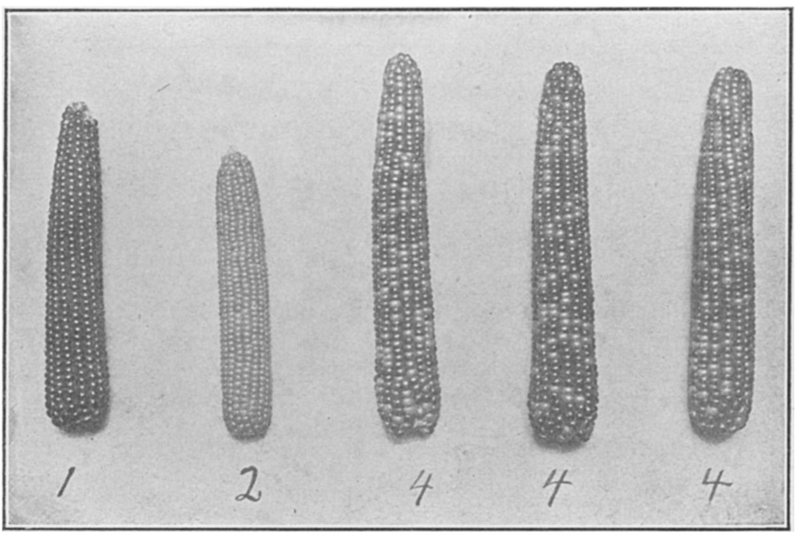

FIG. 2.

ears produced as the result of the cross (F_1) and the second generation hybrid ears (F_2), together for comparison (Figs. 1 and 2; McCluer's Plates 1 and 2). Each of these is a dent-sweet-corn cross, and the results, both of F_1 dominance and of segregation in the F_2 ears, is very plainly shown. In McCluer's Plate 4 the results of segregation are shown, so far as the reappearance of parental types is concerned. Of course, in all these crosses, it must be remembered that the parental types were not selfed strains, but were undoubtedly heterozygous for some of the factors under observation. This is shown in the white corn ear, coming out of a cross between Leaming (yellow dent) and Mammoth Sweet.

The ears shown as types of the varieties used in crossing are selected typical specimens of the varieties, and the ears shown as grown from the crossed seed are typical of the cross-bred corn (p. 95).

McCluer makes the penetrating remark regarding the production of F_2 seeds that

The self-fertilized ears showed the same modification of kernels as those naturally fertilized, proving that *each kernel of the crossed corn, had in itself the power to produce both sweet and dent corn* (p. 95).

In the writer's opinion, *this is the most remarkable expression upon the nature of heterozygosis made before Mendel's time.*

The reappearance of parental types is referred to as follows:

Where the parent varieties were widely different, as in the crosses between sweet and dent, the progeny has tended strongly to run back to the parent forms, while at the same time taking on other forms different from either (p. 95).

A further indirect comment on the superiority in size on the part of F_1 hybrids is seen in McCluer's statement that

Nearly all the corn grown a second year from the crosses is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties (p. 96).

McCluer comments emphatically on the inferior condition of the self-fertilized plants and remarks:

The table giving the weight of ten selected ears of corn from self-fertilized seed, and of ten ears from crossed, or from selected seed, does not give a correct idea of the inferiority of the corn from self-fertilized seed, because it does not take into account, either the greater proportion of abortive stalks, or of small and poorly filled ears (p. 98).

The fact is noticed that some varieties, when crossed, give rise to plants of increased size, while others do not.

Among other incidental matters, McCluer calls attention to the necessity for "A more perfect knowledge of the development of the races and varieties of corn," and wisely remarks regarding the farmer's part in corn breeding:

In the production of new varieties by crossing, it will seldom be desirable to cross two varieties that are very widely different from each other. It is probable that, on the whole, selection, with occasional partial changes of seed, will give more permanent as well as more satisfactory results for the general farmer, than would the continual crossing and breaking-up of well fixed types; though there does seem reason to believe that the crossing of such distinct and well-fixed types, will, for the time being at least, give larger corn and better yields (p. 98).

From McCluer's observations on the results in the second generation of the hybrids he comes to the following intelligent conclusion:

This work gives us a clew to the relative prospects of improvement in other lines by cross-breeding. A variety or type that is strongly fixed is more apt to transmit characters than one poorly or not at all fixed. If we should try to improve corn by crossing the product of two of these cross-bred groups of corn, we should expect to get as a result a few superior ears, with a very large proportion of inferior ones. Even in our well-selected varieties that have been picked for years with reference to given points of excellence, the tendency to run back to inferior forms is so strong, that the grower would save hardly one-tenth of his crop for his own seed. If our well-selected varieties deteriorate thus, when constantly and carefully selected, two varieties that have been long selected for opposite or widely different qualities, must, when crossed, tend to neutralize most strongly the very traits which we have, with so much pains, brought out and maintained.

If, on the other hand, the varieties crossed have long been selected on the same or very similar lines, there seems to be no reason why occasional crossing will not tend to fix more strongly the desired characters.

Here, of course, McCluer quite naturally overlooks the fact of dominance, and adheres, although with a more rational reason than most plant breeders of his time, to the idea of fixation of type through the effects of selection. McCluer, however, here as throughout his paper, shows the inherent instincts of a geneticist, and his paper, although an obscure contribution to the literature of plant breeding, deserves special notice on that account.

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